POPULATION ECOLOGY

Gypsy Moth (Lepidoptera: Lymantriidae) Flight Behavior and Phenology Based on Field-Deployed Automated Pheromone-Baited Traps

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Environ. Entomol. 38(6): 1555-1562 (2009)

ABSTRACT Populations of the gypsy moth, Lymantria dispar (L.), are extensively monitored in the United States through the use of pheromone-baited traps. We report on use of automated pheromone-baited traps that use a recording sensor and data logger to record the unique date-time stamp of males as they enter the trap. We deployed a total of 352 automated traps under field conditions across several U.S. states over a 5-yr period. In many cases, there was general congruence between male moth capture and the number of recorded events. Although it was difficult to decipher an individual recording event because of the tendency for over-recording, the overall distribution of recorded events was useful in assessing male gypsy moth flight behavior and phenology. The time stamp for recorded events corroborated a previous report of crepuscular gypsy moth male flight behavior, because, although most moths were trapped between 12 and 16 h, there was a consistent period of flight activity between 20 and 22 h. The median male flight duration was 24 d (228 DD, base threshold = 10°C), but there were several traps that recorded flight periods >42 d that could not be explained by overcounting given the congruence between moth capture and the number of recorded events. Unusually long flight periods could indicate the introduction of male moths or other life stages that developed under different climatic conditions.

KEY WORDS Lymantria dispar, flight behavior, phenology, sampling, automated trapping

Implementation of insect pest management strategies depends on the ability to characterize the abundance and seasonality of populations. Consequently, monitoring efforts are of prime importance. In many insect species, traps baited with semiochemicals, such as synthetic pheromones, provide a reliable and costeffective method of sampling (Silverstein 1981, Ridgway et al. 1990, Flint and Doane 1996). In the case of the gypsy moth, Lymantria dispar (L.), pheromonebaited traps are deployed under two USDA gypsy moth management programs. One program, Slow the Spread, aims to monitor the progression of the leading population edge as it continues to invade the United States (Tobin and Blackburn 2007), whereas the other, eradication programs, aims to detect newly arrived populations in areas far from its established distribution (USDA 2001, Hajek and Tobin 2009). Between these two management efforts, ≈250,000 traps are placed annually across the continental United

States to detect incipient colonies of gypsy moth, some of which are targeted for management and to estimate population density. These traps are very effective at low population densities. The pheromone is also very specific and generally attracts only gypsy moth males and is stable over time so that it does not need to be replaced during the course of the flight season.

The gypsy moth is a univoltine defoliator that can feed on >300 species of deciduous and coniferous host trees, and preferred host species include oak, willow, and aspen (Elkinton and Liebhold 1990, Liebhold et al. 1995). In North America, females do not fly and oviposit in close proximity to the site of adult emergence (Odell and Mastro 1980). Dispersal is mostly accomplished though male moth flight, early instar ballooning, and the anthropogenic movement of life stages (Doane and McManus 1981, Elkinton and Liebhold 1990, Hajek and Tobin 2009). Unlike many sampling programs conducted in support of integrated pest management (IPM), the goal of gypsy moth trapping is to detect incipient populations and estimate population abundance (USDA 2001, Tobin and Blackburn 2007), as opposed to determining the appropriate timing of management decisions (Elkinton and Cardé 1981). However, the timing of trap deployments is a critical issue, especially because gypsy moth monitoring programs occur over a geographically large and climatically diverse area; thus, the appropriate time to

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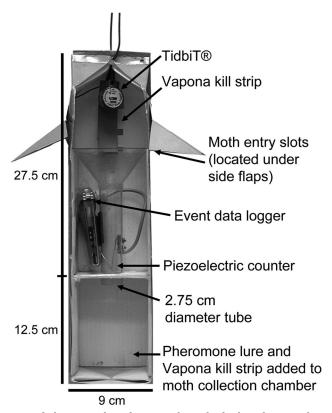


Fig. 1. Design of the automated pheromone-baited traps. Male moths displace the piezoelectric counter, for which the date-time stamp is recorded by an event data logger, when passing through the tube toward the pheromone source in the collection chamber.

set and remove traps is considerably variable depending on the location being monitored. The Slow the Spread monitoring area extends from Minnesota to North Carolina, whereas eradication programs monitor for gypsy moth west and south of the Slow the Spread. Consequently, gypsy moth males can be generally active in flight from June (e.g., North Carolina) to September (e.g., northern Minnesota) depending on local climatic conditions.

Fortunately, gypsy moth monitoring programs have the luxury of several robust phenology models that can be used to predict the occurrence of lifecycle events (Johnson et al. 1983; Logan et al. 1991; Sheehan 1992; Gray et al. 1995, 2001; Régnière and Sharov 1998; Gray 2009). In the Slow the Spread Program, 30-yr mean temperature data are interpolated over a digital elevation model and used to predict the dates of male moth flight over the area being monitored (Régnière and Sharov 1998, Régnière and Sharov 1999, Roberts and Ziegler 2007). These predicted dates are used to approximate the timing of trap set and removal. However, because gypsy moth male moth flight can vary because of year-to-year variation in climate, we sought to address behavior and phenology of gypsy moth flight over a geographically diverse landscape to refine current phenological predictions. Classically, this has been accomplished through the use of sentinel traps that are manually and regularly checked, which is a labor-intensive solution.

An alternate approach is to use an automated sampling device. There have been previous reports of the use of automated sampling devices for monitoring insect populations (Hagstrum et al. 1996, Arbogast et al. 2000, Epsky and Shuman 2000, Maghirang et al. 2003), other animal populations (Sabol and Hudson 1995, Bernatas and Nelson 2004), and automated pheromone-baited traps to monitor other Lepidoptera (Schouest and Miller 1994). In this paper, we report on a 5-yr field deployment of automated pheromone-baited traps to monitor the gypsy moth and describe the behavior and phenology of male moth flight.

Materials and Methods

Automated Pheromone-Baited Trap Design. Automated pheromone-baited traps were developed and initially tested by the USDA Animal and Plant Health Inspection Service, Pest Survey Detection and Exclusion Laboratory, OTIS Air National Guard Base, MA. The trap (Fig. 1) is a modified milk carton trap (USDA 2001) containing a piezoelectric counter interfaced with an event data logger (Onset Computer, Bourne, MA). One synthetic pheromone lure was placed in each collection chamber (USDA 2001). On entry

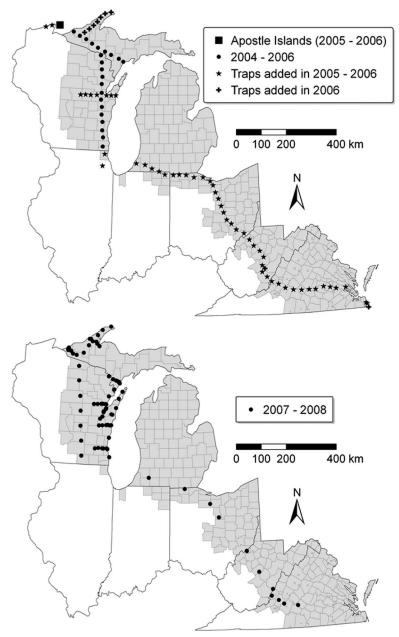


Fig. 2. General locations of deployed automated pheromone-baited traps in 2004–2006 (top) and 2007–2008 (bottom). Counties that are under quarantine for the gypsy moth as of January 1, 2008 are shaded as a reference of the current gypsy moth distribution (U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45-3).

through side slots, a male moth navigates through a tube toward the collection chamber, and when the moth displaces the piezoelectric counter located near the end of the tube, the date and time stamp is recorded by the event data logger. Vapona kill strips (Dichlorvos; 2,2-dichlorovinyl dimethyl phosphate [DDVP]) were placed above the collection chamber (to deter predators) and in the collection chamber (to deter predators and kill male moths; Fig. 1). Each trap also contained a HOBO TidbiT temperature data log-

ger (Onset Computer) to record local temperature conditions.

Field Deployment. A total of 30, 81, 81, 80, and 80 automated traps were placed in the field in 2004, 2005, 2006, 2007, and 2008, respectively (Fig. 2). These traps were placed along the leading edge of the current gypsy moth distribution, where expected densities generally range from 50 to 300 moths per trap as ascertained by the placement of traps through the Slow the Spread Program (Decision Support System

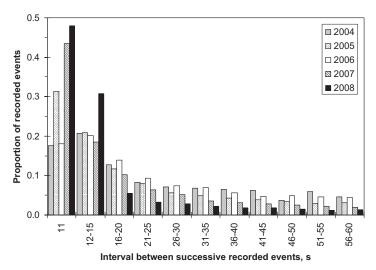


Fig. 3. Distribution of the time interval between successive recordings. Traps were deployed with a 10-s delay so the minimum interval is 11 s. Note the high proportion of events recorded exactly 11 s apart.

for the Gypsy Moth Slow the Spread Program 2009). Automated pheromone-baited traps were always placed at least 1 km away from the nearest standard trap deployed under Slow the Spread. Most traps were placed along a general southeast-to-northwest or north-to-south transect from North Carolina to the Upper Peninsula of Michigan, although some were placed along transects emanating from Lakes Michigan and Superior to account for lake-mediated climatic effects (Fig. 2).

Automated pheromone traps were deployed from May to June, beginning with the most southern located traps, and removed in August to October, ending with the most northern traps. On trap placement, spatial coordinates were recorded using GPS. The piezoelectric counter was set with a 10-s delay so that successive recordings had to be at least 11 s apart. A delay was used because it was not known a priori the time a male moth would require to navigate through the tube and into the collection chamber of the trap (Fig. 1). In the first year of deployment (2004), automated traps were checked in mid-August to count the number of moths trapped and recorded events as part of a preliminary validation of their use. After trap removal, the number of moths in each trap was counted through visual inspection, and the number of events recorded by the event logger was downloaded.

Temperatures were recorded by the HOBO TidbiT data logger (Onset Computer) every 30 min and were used to estimate the degree-day accumulation (base threshold = 10°C) during the male flight period. Degree-day accumulation was estimated using the trapezoidal method of integration, derived from the first three terms of the Taylor series expansion (Tobin et al. 2001), applied to each 30-min interval.

Data Analyses. The correlation between the number of males trapped and the number of recorded events in each automated pheromone-baited trap was determined using Pearson's correlation coefficient. The time stamp associated with events was used to understand the timing of flight behavior. Follow-up analyses were conducted on a subset of traps in which there was a reasonable congruence between moth capture and recorded events, which we defined as those traps in which the ratio of moths-to-events was \geq 0.8:1 and \leq 1.2:1 and for which at least 30 moths were trapped. In this subset, we examined the relationship between the latitude at which the trap was deployed and the estimated 5, 50, and 95% dates of recorded events using least squares regression. The relationship between latitude and male moth flight duration, bounded by the estimated dates of 5 and 95% of recorded events, when represented as days and degreedays, was also assessed using least squares regression. All statistical analyses were conducted in R (R Development Core Team 2007).

Results and Discussion

A total of 27 of 30, 49 of 81, 62 of 81, 69 of 80, and 50 of 80 of the automated pheromone-baited traps were recovered with usable data from 2004 to 2008, respectively. Traps without usable data were those that did not catch any moths, were destroyed by wildlife or vandalized, experienced mechanical failure in the event data logger, or were inhabited by other species such as crickets, mice, or spiders that made it impossible to count accurately the number of moths. Also, some traps placed in high-density areas were unusable because the number of male moths was so high that the tube in the trap was completely clogged with moths such that very few moths actually made it into the collection chamber. Thus, given the diameter of the tube (2.75 cm; Fig. 1), this type design would not be appropriate for measuring extremely high density populations (i.e., outbreak populations). Data from all these traps were omitted from our initial analyses.

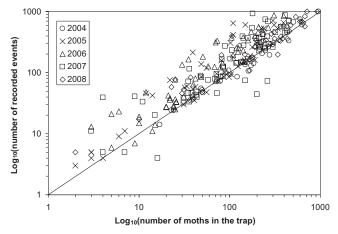


Fig. 4. Relationship between the number of moths and the number of recorded events, 2004–2008. Each symbol represents one trap, and the diagonal line represents the 1:1 relationship.

We used initially a 10-s delay for recording events in the event data logger, but we were also interested in approximating the appropriate delay. We thus examined the distribution of intervals between successive recording events, and in all years, an interval duration of exactly 11 s was greatly over-represented. Among all intervals from 11 to 60 s, when partitioned into 1-s intervals, the interval 11 s accounted for 40.8% of observations, whereas the interval 11-15 s accounted for 63.4% of observations. A distribution of the interval between successive recording events in shown in Fig. 3, which shows less variation in recorded events among interval classes (i.e., 11, 12–15, 16–20, . . . $56-60 \,\mathrm{s}$) at intervals $>30 \,\mathrm{s}$. This suggests that for these data, a 30-s delay may be more appropriate when recording gypsy moth events. However, because it is difficult to predict the time required for a gypsy moth male, or any other insect, to successively pass through the tube and into the collection chamber, it would be prudent to deploy the traps with a short delay and attempt to deduce a more appropriate

delay through exploratory data analysis (Fig. 3) or other methods. For example, future laboratory and field experiments could be developed to measure the required time for moths to navigate through the tube and to determine the effect of male moth density on the expected time between successive moth captures.

Because of the relationship presented in Fig. 3, we used an event recording delay of 30 s when counting the number of recorded events and compared this value with the number of male moths collected in each trap. Although several traps recorded events that were nearly identical to the number of moths in the trap, there was a tendency for overcounting (Fig. 4), even though there was still a strong significantly positive correlation between moths trapped and recorded events ($\rho = 0.77$; df = 256; P < 0.0001). Based on the time stamp of recorded events, peak male moth flight generally occurred between 12 and 17 h (Fig. 5), which is consistent with previous observations (Cardé et al. 1974). There was also a smaller yet consistently

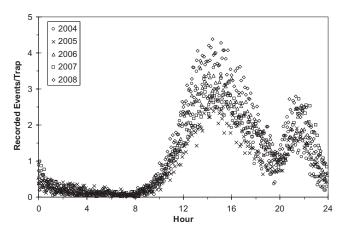


Fig. 5. The number recorded events per trap over time. Note the periodicity in the timing of male moth flight behavior and evidence of crepuscular activity.

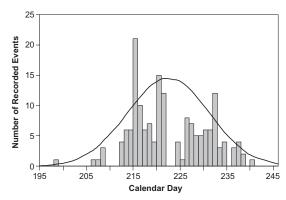


Fig. 6. Example flight curve based on the daily distribution of recorded events, showing the utility of these traps in modeling phenology even when event data are imperfect. A Gaussian distribution is fit to these data as an example.

observed crepuscular peak between 21 and 22 h (Fig. 5), which has also been previously observed (Odell and Mastro 1980). Giebultowicz et al. (1992) reported that peaks of pheromone titer in females occurs more toward the evening hours with increasing female age, which may provide an explanation for male crepuscular flight activity.

Our subset consisted of 80 automated traps, for which the overall mean ratio of moths to recorded events was 0.98:1, whereas the correlation between trapped moths and recorded events was highly positively significant ($\rho = 0.99$; df = 79; P < 0.0001). Phenological assessments were conducted on this subset, and an example of the phenological distribution for one of the traps is presented in Fig. 6. The gaps in the distribution of recorded events could reflect unfavorable climatic conditions on certain days that may restrict male moth flight. The calendar day of 5, 50, and 95% male flight by latitude is shown in Fig. 7. The slopes for the least squares regression fits to each flight percentile were not significantly different (F = 0.04; df = 1,236; P = 0.95), and the common slope was 3.8 (SE = 0.05); thus, for each degree of latitude, the calendar day at which 5, 50, or 95% of male flight occurs increases by ≈ 3.8 d. These results are similar to those reported by Régnière and Sharov (1998), who noted the differences in the timing of male moth flight over elevation and reported an increase of 3.3-4.4 d in observed median male moth flight for each 100 m of elevation.

When considering the total male moth flight period (i.e., the period between the 5th and 95th percentiles of male moth flight), the median of the flight period was 24 d and 228 DD (Fig. 8). There was no significance difference in the duration of male moth flight across latitude, whether days (F = 0.01; df = 1,78; P =0.94) or degree-days (F = 2.08; df = 1,78; P = 0.15) were considered. However, although most traps recorded flight periods <6 wk, 13 of the 80 traps had flight periods ≥6 wk, including a maximum of 93 d and 833.5 DD (Fig. 8). Because it is extremely unlikely that local gypsy moth male populations would exhibit flight over such an extended period, it is possible that males, perhaps facilitated through atmospheric transport mechanisms, dispersed into some of these areas after developing under another area's climatic conditions. Alternatively, the extended male flight period could be because of immature life stages that were anthropogenically introduced, providing that they completed enough development under different climatic conditions to remain asynchronous with the timing of male emergence from resident populations.

Automated sampling devices provide many benefits to IPM programs, which often depend heavily on sampling efforts. Sensors and data loggers that can be incorporated into trapping devices offer an opportunity to greatly enhance our understanding of flight behavior and phenology for a specific insect species and to model these relationships in spatially and temporally explicit detail. Our primary objective in this paper was to present a summary of the utility of automated pheromone-baited traps for monitoring gypsy moth populations, technology that can be transferred to other systems, and to provide an assessment of male moth flight behavior and phenology. Future

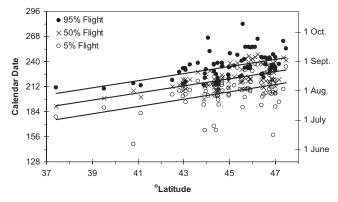


Fig. 7. Dates of 5, 50, and 95% of flight across latitude. Lines are the least squares regression fits (95 to 50 to 5%, top to bottom). Each degree of latitude resulted in a shift of \sim 3.8 d in the expected date of 5, 50, and 95% male moth flight.

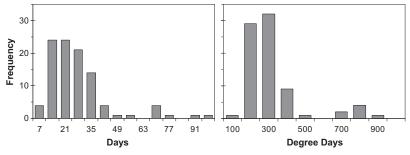


Fig. 8. Frequency distribution of the number of automated traps over the duration of male moth flight (i.e., 5–95% of male flight) based on calendar days and degree days. The median duration of flight was 24 d and 228 DD (base threshold = 10° C).

studies will examine the phenological aspects of these data in greater detail.

Acknowledgments

We thank A. Sawyer (USDA Animal and Plant Health Inspection Service) for developing the automated traps and L. Blackburn and G. Racin (USDA Forest Service), C. Lettau (Wisconsin Department of Agriculture Trade and Consumer Protection), and K. W. Thorpe (USDA Agricultural Research Service) for assistance. This research was financially supported by the USDA Forest Service, Forest Health Protection, and the Gypsy Moth Slow the Spread Foundation.

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Received 11 February 2009; accepted 5 August 2009.